



Phosphorus acquisition and utilisation in crop legumes under global change

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Improving phosphorus (P)-use efficiency in legumes is a worldwide challenge in the face of an increasing world population, dwindling global rock phosphate reserves, the relatively high P demand of legumes and global change. This review focuses on P acquisition of crop legumes in response to climate change. We advocate further studies on: firstly, the response of carboxylate exudation, mycorrhizas and root morphology to climate change and their role in P acquisition as dependent on edaphic factors; secondly, developing intercropping systems with a combination of a legume and another crop species to enhance P acquisition; and thirdly, the impact of the interactions of the major climate change factors on P acquisition in the field.

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Introduction

Crop legumes are not only important food and feed sources, but they play a significant role in the sustainability and productivity of cropping systems [1]. They contribute to cropping system diversity when grown with crops of other plant families, disrupting the pest and disease cycles that develop with continuous cropping of one species [2[•],3[•]]. If effectively nodulated, legumes can significantly enhance nitrogen (N) input into cropping systems [4]. Many crop legumes release sparingly-available soil phosphorus (P), possibly increasing the plant-available P pool for the entire cropping system [5[•],6].

Phosphorus is a structural component of nucleic acids, coenzymes, phospholipids and sugar phosphates [7,[10[•]]]. It also plays a pivotal role in N₂ fixation [9]. Food production to support a growing world population requires a large input of P fertiliser, which is manufactured from non-renewable resources expected to diminish significantly in the next century [10[•]]. However, the P supplied in fertiliser is used very inefficiently, with, worldwide, only one-fifth of the P mined being consumed due to huge losses and inefficiencies from mine to field to fork [11]. While intensification of agriculture in many countries has led to P-saturated soils and resulting environmental problems [12[•]], P deficiency still limits crop production in many regions [13[•]]. Given an expected global human population of 9.7 billion by 2050, there is an urgent need to develop strategies to use world P reserves more wisely, that is, greater yields per unit of added P. Development of more P-efficient legume crops is therefore important.

Climate change has brought impacts for agricultural production through increasing atmospheric CO₂ concentrations, warmer temperatures, increased or decreased precipitation depending on region, and increased climatic variability within years [14]. Global climate change may impact plant growth and nutrient demand, and soil nutrient availability. Understanding P acquisition in legume crops under climatic change will be crucial for developing more P-efficient farming systems. For crop plants, P-use efficiency comprises two components — P-acquisition efficiency and P-utilisation efficiency, that is, the production of dry matter per unit P in the plant. This review primarily focuses on P acquisition of crop legumes.

Many sub-traits affect P acquisition, including: root architectural and morphological specialisations; release of protons, carboxylates and phosphatases into the rhizosphere; and the ability to associate with mycorrhizal fungi [15,16]. Legumes generally require more P than non-legumes, partly because N₂-fixing root nodules are strong P sinks [17]. Different genotypes rely on a different mix of strategies. For example, for common bean (*Phaseolus vulgaris*) and soybean (*Glycine max*), genotypes with shallow basal root growth angle — associated with enhanced topsoil foraging — exhibit superior P acquisition in low-P soils compared with genotypes with steep angles [18,19]. In pasture legumes [20] and common bean [21], long root hairs and a large root-hair-cylinder surface area enhance P acquisition. Root hair length and shoot P content appear unrelated in chickpea (*Cicer arietinum*), perhaps because

the release of organic anions is relatively more important [22**].

Effects of water stress on P acquisition Root morphology, carboxylates and arbuscular mycorrhizal fungi (AMF)

Water stress is the most common yield-limiting abiotic stress in legume production [23]. Phosphate in soil moves very slowly via diffusion, at about 0.1 mm per day. If the soil water content decreases, the radii of water-filled pores decrease, tortuosity increases, and P mobility decreases [24], leading to 'P nutritional drought'. Phosphate in soil also moves via mass flow driven by plant transpiration, and this rate also declines with decreasing soil moisture content [25]. Water stress decreases stomatal conductance, and therefore often increases leaf temperature, for example, in bean (*P. vulgaris*) and red clover (*Trifolium pratense*) [26], implying that stomatal closure induced by water stress is often accompanied with increased temperature stress. Leaf P concentration and transpiration rate of young fully expanded leaves were strongly correlated in a large set of chickpea genotypes with diverse genetic background grown in sand with a low P concentration and low P-buffering capacity. This indicates involvement of stomatal conductance and a contribution of transpiration-driven mass flow to P acquisition [27**]. Therefore, we hypothesise that decreased stomatal conductance induced by water stress will reduce mass flow and its role in P acquisition in legumes grown in soils with low-P buffering capacity, that is, in sandy soils. Soil moisture is also important for microbial P supply from organic sources. Therefore, reduced P mobility and availability during dry periods often co-occur with decreased root activity [28].

Root foraging in top soil is considered an effective strategy for P acquisition, because P is mostly concentrated in the top layers [29]. In response to water stress, some legumes change their investment strategy to favour accessing water over P, that is, investing in deeper roots to acquire water rather than P [30]. For example, for common bean, shallow-rooted genotypes grow relatively better under P stress, deep-rooted genotypes grow better under water stress, while genotypes with a dimorphic root system permitting vigorous rooting throughout the soil profile grow best in the combined stress treatment [31]. The authors suggest that architectural plasticity and root dimorphism through complementary growth of distinct root classes may be important to enhance acquisition of multiple soil resources.

Some legumes, for example, chickpea, exude large amounts of carboxylates into the rhizosphere [22**]. Few studies are available on rhizosphere carboxylates under water stress for legumes, with inconsistent results — water stress increased the amount of carboxylates per gram root dry weight in rhizosheaths in two

lucerne (*Medicago sativa*) cultivars [32] and three perennial pasture legumes (*M. sativa*, *Cullen australasicum* and *C. pallidum*) [33]. In contrast, the amount of carboxylates per gram root dry weight was less under water stress for *C. australasicum* and *M. sativa* in another study [34]. These differences were attributed to microbial degradation, restricted diffusivity of rhizosphere carboxylates and/or possible death or reduced activity of fine roots in dry soil layers [34]. The composition of carboxylates may also shift in response to water stress, for example, all legume species shifted from citrate in the well-watered control to malate under water stress, possibly due to differences in exudation rates, diffusivity and/or half-life of rhizosheath carboxylates [33]. No quantitative evidence exists on the beneficial effects of carboxylates, or impact of the compositional shift, on P acquisition under water stress; this needs to be explored.

Mycorrhizal colonisation of legume crops under water stress and its role in P acquisition, particularly in field conditions is poorly known [35*,36]. In a controlled environment, AM symbiosis increased resistance to water stress in white clover (*Trifolium repens*) [37] and protected against premature water-stress-induced nodule senescence in soybean [38]. In the field, application of AMF increased dry matter production, grain yield, and shoot P concentration of legumes, including cluster bean (*Cyamopsis tetragonoloba*), mung bean (*Vigna radiata*) and moth bean (*V. aconitifolia*) grown in water-stress-prone areas of Western Rajasthan in India with low soil P levels [39], and for chickpea grown in a rain-fed low-input cropping system in Italy [40]. Since rainfall or soil moisture levels during the growing season were not described in these studies, it is unknown whether plants experienced water stress. More direct evidence on the effects of mycorrhiza on P acquisition and grain yield is needed, particularly under field conditions, both dry and with ample water. Further research on the mechanisms underlying the protective role of AMF against water stress and P acquisition would be helpful.

Hydraulic redistribution

Some legumes, especially perennial legumes, are often deep-rooted and show hydraulic redistribution [38,39]. However, it is very hard to unequivocally ascribe effects on nutrient uptake of intercropped plants to hydraulic redistribution. Hydraulic lift was observed in deep-rooted pasture legumes (*M. sativa* and *C. pallidum*); survival of interplanted shallow-rooted *T. subterraneum* was greater, but there was no facilitation of P or Rb uptake [41]. To take advantage of hydraulic redistribution under water stress and its potential role in enhancing P acquisition, new agricultural systems are required. For example, in a field experiment [42*], the negative effects of interspecific competition for water were eliminated by subjecting deep-rooted pasture plants to complete shoot removal to stop transpiration which forced the pasture into a passive

nurse role and increased the dry matter production of shallow-rooted crops in a water-limited environment.

Elevated CO₂

Plant growth and P acquisition

The advent of Free Air CO₂ Enrichment (FACE) facilities has improved our understanding of plant response to CO₂-enriched environments. Elevated CO₂ (eCO₂) may act as a carbon fertiliser to enhance photosynthetic rate and increase productivity [43]; N₂-fixing species generally respond more than non-fixing species [44]. However, eCO₂ tends to decrease shoot P concentration [45,46], shoot N concentration and the enzyme Rubisco [47], which represents the major fraction of N in leaves [48], such that less P is required for rRNA, a major component of organic P in leaves [8,49^{*}]. Alternatively, decreased shoot P concentration often observed under eCO₂ may indicate that not enough nutrients can be delivered to the shoots, therefore limiting the plant's capacity to fix the extra CO₂ available in the atmosphere. As a result of increased plant growth and a smaller proportion of P in leaves used for photosynthesis-associated metabolisms, P-use efficiency should increase under eCO₂. Excess sugars produced from photosynthesis should increase the C investment belowground, for example, for root growth, carboxylate exudation and mycorrhizal colonisation, to enhance P-acquisition efficiency.

To facilitate the positive effects of eCO₂, appropriate management of P fertiliser is crucial. For example, chick-pea and field pea (*Pisum sativum*) grown in FACE increased plant growth, nodule biomass, N₂-fixation and total P uptake under 16 mg P kg⁻¹ soil in response to eCO₂, but not under nil-P [50^{*}]. Due to the differential response of crop species/genotypes to eCO₂, the selection of appropriate germplasm is important. Genetic resource selection (G) and agronomic management (M), and the local environment (E), need to be considered; field evaluation is essential.

Since eCO₂ increases photosynthesis and decreases leaf stomatal conductance and transpiration [51], water-use-efficiency improves under eCO₂. Similar to our hypothesis that decreased stomatal conductance induced by water stress reduces P acquisition, we also hypothesise that decreased stomatal conductance induced by eCO₂ will reduce mass flow and its role in P acquisition in legumes grown in soils with low-P buffering capacity, that is, sandy soils. This needs to be further tested in other legumes.

Root morphology, rhizosphere carboxylates, and AMF

Elevated CO₂ generally increases C allocation to roots and stimulates root growth — including changes in root architecture and morphology — enabling roots to explore a larger volume of soil and increase P acquisition [50^{*}]. Most studies on changes in root morphology in response to eCO₂ are limited to root biomass and root length.

Cluster root production is affected by CO₂, for example, in white lupin the number, biomass and percentage of cluster roots increased under eCO₂ [52] and cluster rootlets reach a shorter final length one day earlier under eCO₂ [53]. The physiological and molecular mechanisms underlying root development in response to eCO₂ remain largely unknown.

The limited studies, mostly in FACE, under eCO₂ show greater carboxylate release into the rhizosphere, for example, in common bean [54]. Citrate exudation from cluster rootlets of white lupin grown under eCO₂ starts a day earlier and lasts a day less [53]. Overall, exudation may increase because root production increases under eCO₂, but there is no direct evidence. Carboxylate exudation from roots under eCO₂, and its contribution to P mobilisation in the rhizosphere, needs to be assessed, particularly under field conditions.

The benefits of carboxylates for P acquisition may be best captured through use of intercropping system. For example, on P-deficient soils in the field, both intercropped maize (*Zea mays*) and faba bean (*Vicia faba*) over-yield. Maize over-yielding is attributed to its uptake of P mobilised via organic acid release by faba bean roots [5^{**}]. In addition, root exudates from maize promote faba bean nodulation and stimulate N₂ fixation; faba bean roots treated with maize root exudates had an 11-fold increase in the expression of the chalcone-flavonone isomerase gene involved in flavonoid synthesis and increased expression of genes mediating nodulation and auxin response; wheat (*Triticum aestivum*) or barley (*Hordeum vulgare*) exudates do not have this effect [55^{**}].

Elevated CO₂ often stimulates the growth of AMF under P-deficient conditions, for example, in *Trifolium repens* [56]. The abundance of AMF relative to root length increased by 47% under eCO₂ in a meta-analysis [57]. Different AMF may respond differently to eCO₂. For instance, AM colonisation increased for *Deschampsia flexuosa* and *Calluna vulgaris* in nutrient-limited heathlands, while ericoid mycorrhizal colonisation was unchanged under eCO₂ [58]. There is little information on the role of AMF in plant nutrient acquisition under eCO₂. Cheng *et al.* [59] showed that eCO₂ enhances mycorrhizal N transfer from decomposing organic material to host plants. However, the mycorrhizal transfer of P to host plants is unknown. The increased symbiotic activity between AMF and plants under eCO₂ leads to a hypothesis that mycorrhizal plants in P-deficient soils will perform relatively better than non-mycorrhizal ones.

Effects of increasing temperature on P acquisition

Temperature is important in determining the length of the growing season, with different legume species having different optimal temperatures [60]. Rising temperatures

will likely increase yields in cooler areas and decrease yields in warmer areas [61].

Although there have been a large number of studies on the rising temperature on legume growth and development, knowledge on the effects of rising temperatures on root morphology, rhizosphere carboxylate concentration and composition, and the impact on P uptake and growth is limited for legume crops. Three herbaceous legume species exhibited different root morphological and carboxylate responses to temperature treatments [60]. For *Kennedia nigricans* and *Lotus australis*, carboxylate amounts declined when grown under temperatures higher than their optimum [60]. This was not the case for *Cullen cinereum*, which instead had long, thin roots with higher specific root length to explore a greater volume of soil at optimum temperatures. *Kennedia nigricans* had the highest root mass ratio at optimal temperature which declined at higher temperatures.

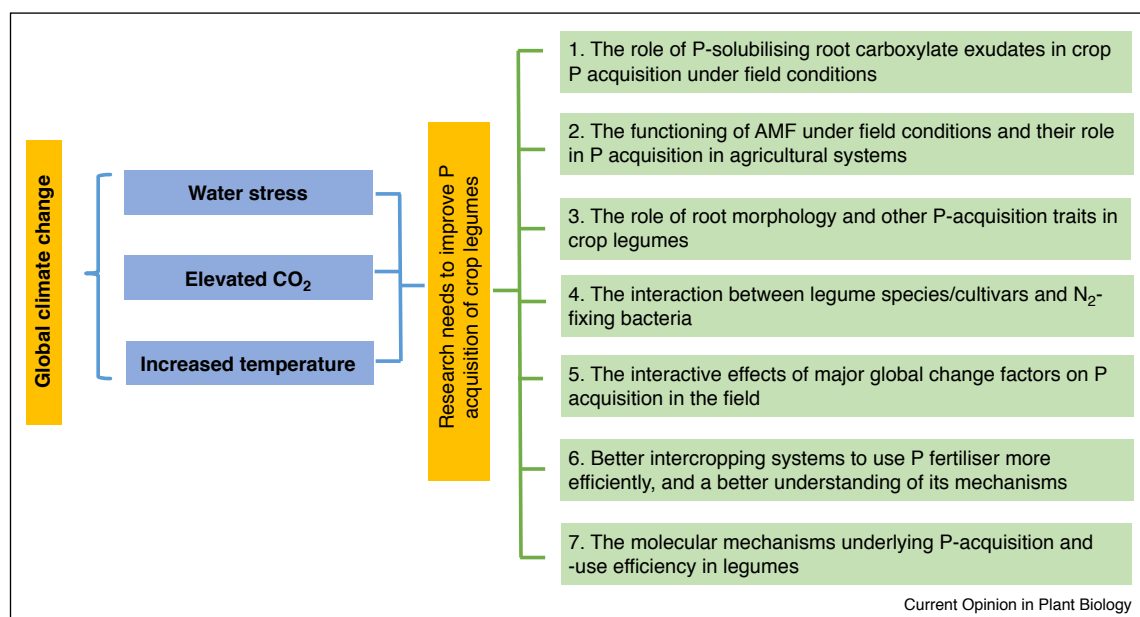
Perspectives

Phosphorus acquisition involves many belowground and aboveground–belowground interactions (Figure 1). We know little of the effects of climate change on P requirement and P-acquisition in legumes under different soil types and climate conditions. There is no information on variation in P requirements in crop legumes for nodule functioning and N₂ fixation. With the increasing world population and declining global rock phosphate reserves, there is an urgent need to improve crop P-acquisition and

P-use efficiency. We suggest the need for more information, specifically:

- 1) Enhanced understanding of the role of P-solubilising root carboxylate exudates in crop P acquisition under field conditions for crop legumes (in cluster-rooted and non-cluster-rooted species). The role of carboxylates in intercropping systems particularly deserves further attention.
- 2) A better understanding of the functioning of AMF under field conditions in crop legumes and their role in P acquisition in agricultural systems. The crop agronomy literature rarely reports a positive benefit from AMF for yield [62]. Few mycorrhizal studies have measured yield or other variables to analyse agronomic gains, and AMF are rarely deliberately managed in agroecosystems.
- 3) We need to continue to improve our understanding of root morphology and other P-acquisition traits in crop legumes, noting that crops/genotypes will differ in their suite of traits, and that P availability may change the balance of key traits.
- 4) As N₂ fixation is often enhanced by eCO₂, but inhibited by abiotic factors such as water stress and increased temperature, studies of the interactions between legume species/cultivars and N₂-fixing bacteria and their impacts on P acquisition under climate change will be important to enhance symbiotic N₂ fixation.
- 5) Few studies have examined the interactive effects of major global change factors on P acquisition. The

Figure 1



Future research priorities to improve phosphorus (P) acquisition of crop legumes in face of climate change.

combined effects of water stress, increased temperature and eCO_2 often counteract the main effects of soil nutrient mineralisation and immobilisation, suggesting a need to investigate interactive effects among climate change factors [63]. As Long *et al.* pointed out [64], current projections of global food security might be overoptimistic as the fertilisation effects of CO_2 may be less than that used in many models, and other factors such as rising atmospheric ozone concentrations may cause yield losses.

- 6) We need to design better mixed cropping systems, that is, systems with diverse rotations or intercropping, to use P fertiliser more efficiently, meanwhile minimising loss of P to the environment, and better understanding of their functioning. For instance, maize–grain legume intercropping is more beneficial than monocultures in less fertile fields and more marginal environments such as in the northern Guinea savannah [3*].
- 7) Knowledge of molecular mechanisms for P acquisition in response to water stress, increased temperature and eCO_2 , and their interaction is required to improve P-acquisition and P-use efficiency in legumes.

In summary, we call for a research focus on interactive effects of global change factors on crop yield and P acquisition under field conditions, with consideration of $G \times E \times M$ interactions for crop legumes [65]. Only then will we be able to confidently address negative impacts and maximise benefits from targeted mitigation efforts using crop breeding and management.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as

- of special interest
- of outstanding interest

1. Siddique KHM, Johansen C, Turner NC, Jeuffroy M-H, Hashem A, Sakar D, Gan Y, Alghamdi SS: **Innovations in agronomy for food legumes. A review.** *Agron Sustain Dev* 2012, **32**:45–64.
2. Foyer CH, Lam H-M, Nguyen HT, Siddique KHM, Varshney RK, Colmer TD, Cowling W, Bramley H, Mori TA, Hodgson JM *et al.*: **Neglecting legumes has compromised human health and sustainable food production.** *Nature Plants* 2016, **2**:16112.
- This review emphasises the importance of grain legumes in food security, human health and soil fertility, and technologies for legume improvement, when the United Nations declared 2016 as the FAO International Year of Pulses. The paper highlights the importance of genetic resources and their utilisation in crop improvement programs using molecular and breeding technologies.
3. Kermah M, Franke AC, Adjei-Nsiah S, Ahiabor BDK, Abaidoo RC, Giller KE: **Maize-grain legume intercropping for enhanced resource use efficiency and crop productivity in the Guinea savanna of northern Ghana.** *Field Crops Res* 2017, **213**:38–50.
- This paper shows that the intercrop converts the intercepted radiation more efficiently into grain yield than the sole crops; the economic returns are greater for intercrops than for either sole crop in the Guinea savannah. It also shows that intercropping is more beneficial in less fertile fields and in more marginal environments, although overall cropping is more profitable in fertile fields due to larger absolute grain yields.
4. Plaza-Bonilla D, Nolot J-M, Raffaillac D, Justes E: **Innovative cropping systems to reduce N inputs and maintain wheat yields by inserting grain legumes and cover crops in southwestern France.** *Eur J Agron* 2017, **82**:331–341.
5. Li L, Li S-M, Sun J-H, Zhou L-L, Bao X-G, Zhang H-G, F-S Zhang: **Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils.** *Proc Natl Acad Sci USA* 2007, **104**:11192–11196.
- The authors show that in an intercropping system of maize and faba bean for four years in fields with a low-P but high-nitrogen soil, both maize and faba bean overyielded. Maize overyielding resulted from its uptake of P mobilised by the modification of the rhizosphere via faba bean root release of organic acids, while overyielding of faba bean was because growth season and rooting depth differed from that of maize.
6. Nuruzzaman M, Lambers H, Bolland MDA, Veneklaas EJ: **Phosphorus benefits of different legume crops to subsequent wheat grown in different soils of Western Australia.** *Plant Soil* 2005, **271**:175–187.
7. Raghothama KG: **Phosphate acquisition.** *Annu Rev Plant Physiol Plant Mol Biol* 1999, **50**:665–693.
8. Veneklaas EJ, Lambers H, Bragg J, Finnegan PM, Lovelock CE, Plaxton WC, Price CA, Scheible WR, Shane MW, White PJ *et al.*: **Opportunities for improving phosphorus-use efficiency in crop plants.** *New Phytol* 2012, **195**:306–320.
9. Raven JA: **Protein turnover and plant RNA and phosphorus requirements in relation to nitrogen fixation.** *Plant Sci* 2012, **188**:25–35.
10. Fixen PE, Johnston AM: **World fertilizer nutrient reserves: a view to the future.** *J Sci Food Agric* 2012, **92**:1001–1005.
- This review advocates the development and implementation of fertiliser best management practices with focus on the 4Rs (right source, right rate, right time and right place), which is timely not only for short-term economic and environmental benefits, but also for a wise stewardship of non-renewable nutrient resources.
11. Cordell D, White S: **Tracking phosphorus security: indicators of phosphorus vulnerability in the global food system.** *Food Security* 2015, **7**:337–350.
12. Mekonnen MM, Hoekstra AY: **Global anthropogenic phosphorus loads to freshwater and associated grey water footprints and water pollution levels: a high-resolution global study.** *Water Resour Res* 2018, **54**:345–358.
- This study estimated the global anthropogenic P loads to freshwater and the associated grey water footprints for the period 2002–2010. As agriculture contributes 38% of the P load to freshwater systems, reducing the application of P in agriculture to become more environment-friendly is desirable. Moreover, it is possible without reducing agricultural productivity.
13. MacDonald GK, Bennett EM, Potter PA, Ramankutty N: **Agronomic phosphorus imbalances across the world's croplands.** *Proc Natl Acad Sci U S A* 2011, **108**:3086–3091.
- This paper calculated P balances for cropland soils with production of 123 crops globally for the year 2000 and found massive variation in the magnitude of the P imbalances, that is, P surplus or deficits across most regions, particularly Europe and South America. More efficient use of P fertilisers and more effective recycling of manure P may be a way to resolve agronomic P imbalances.
14. Lobell DB, Gourdji SM: **The influence of climate change on global crop productivity.** *Plant Physiol* 2012, **160**:1686.
15. Lopez-Arredondo DL, Leyva-Gonzalez MA, Gonzalez-Morales SI, Lopez-Bucio J, Herrera-Estrella L: **Phosphate nutrition: improving low-phosphate tolerance in crops.** *Annu Rev Plant Biol* 2014, **65**:95–123.
16. Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ: **Root structure and functioning for efficient acquisition of phosphorus: Matching morphological and physiological traits.** *Ann Bot* 2006, **98**:693–713.
17. Sprent JI: **Nitrogen fixation and growth of non-crop legume species in diverse environments.** *Perspect Plant Ecol Evol Syst* 1999, **2**:149–162.
18. Lynch JP: **Root phenes for enhanced soil exploration and phosphorus acquisition: tools for future crops.** *Plant Physiol* 2011, **156**:1041.

19. Wang X, Yan X, Liao H: **Genetic improvement for phosphorus efficiency in soybean: a radical approach.** *Ann Bot* 2010, **106**:215-222.
 20. Haling RE, Yang Z, Shadwell N, Culvenor RA, Stefanski A, Ryan MH, Sandral GA, Kidd DR, Lambers H, Simpson RJ: **Root morphological traits that determine phosphorus-acquisition efficiency and critical external phosphorus requirement in pasture species.** *Funct Plant Biol* 2016, **43**:815-826.
 21. Yan X, Liao H, Beebe SE, Blair MW, Lynch JP: **QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean.** *Plant Soil* 2004, **265**:17-29.
 22. Pang J, Bansal R, Zhao H, Bohuon E, Lambers H, Ryan MH, ●● Ranathunge K, Siddique KHM: **The carboxylate-releasing phosphorus-mobilizing strategy can be proxied by foliar manganese concentration in a large set of chickpea germplasm under low phosphorus supply.** *New Phytol* 2018 <http://dx.doi.org/10.1111/nph.15200>.
- This study demonstrates that the mature leaf manganese concentration can be used as an easily measurable proxy for the assessment of belowground carboxylate-releasing processes in a range of chickpea genotypes grown under low-P, which offers an important breeding trait for chickpea, with potential application in other crops as well.
23. Farooq M, Gogoi N, Barthakur S, Baroowa B, Bharadwaj N, Alghamdi SS, Siddique KHM: **Drought stress in grain legumes during reproduction and grain filling.** *J Agron Crop Sci* 2017, **203**:81-102.
 24. Faye I, Diouf O, Guissé A, Sène M, Diallo N: **Characterizing root responses to low phosphorus in pearl millet [*Pennisetum glaucum* (L.) R. Br.].** *Agron J* 2006, **98**:1187-1194.
 25. Marschner P, Rengel Z: **Nutrient availability in soils.** In *Marschner's Mineral Nutrition of Higher Plants*, 3rd ed.. Edited by Marschner P. Academic Press; 2012:315-330.
 26. Reynolds-Henne CE, Langenegger A, Mani J, Schenk N, Zumsteg A, Feller U: **Interactions between temperature, drought and stomatal opening in legumes.** *Environ Exp Bot* 2010, **68**:37-43.
 27. Pang J, Zhao H, Bansal R, Bohuon E, Lambers H, Ryan MH, ●● Siddique KHM: **Leaf transpiration plays a role in phosphorus acquisition among a large set of chickpea genotypes.** *Plant Cell Environ* 2018 <http://dx.doi.org/10.1111/pce.13139>.
- This study used a unique set of 266 chickpea genotypes with diverse genetic background to assess variation in P-use efficiency. The authors suggest a role for leaf transpiration in P acquisition, consistent with transpiration-driven mass flow in chickpea grown in low-P sandy soils.
28. Dijkstra FA, Pendall E, Morgan JA, Blumenthal DM, Carrillo Y, LeCain DR, Follett RF, Williams DG: **Climate change alters stoichiometry of phosphorus and nitrogen in a semiarid grassland.** *New Phytol* 2012, **196**:807-815.
 29. Simpson RJ, Oberson A, Culvenor RA, Ryan MH, Veneklaas EJ, Lambers H, Lynch JP, Ryan PR, Delhaize ED, Smith FA et al.: **Strategies and agronomic interventions to improve the phosphorus-use efficiency of farming systems.** *Plant Soil* 2011, **349**:89-120.
 30. Lynch J, Ho M: **Rhizoeconomics: carbon costs of phosphorus acquisition.** *Plant Soil* 2005, **269**:45-56.
 31. Ho MD, Rosas JC, Brown KM, Lynch JP: **Root architectural tradeoffs for water and phosphorus acquisition.** *Funct Plant Biol* 2005, **32**:737-748.
 32. Fan J-W, Du Y-L, Turner NC, Wang B-R, Fang Y, Xi Y, Guo X-R, Li F-M: **Changes in root morphology and physiology to limited phosphorus and moisture in a locally-selected cultivar and an introduced cultivar of *Medicago sativa* L. growing in alkaline soil.** *Plant Soil* 2015, **392**:215-226.
 33. Suriyagoda LDB, Ryan MH, Renton M, Lambers H: **Multiple adaptive responses of Australian native perennial legumes with pasture potential to grow in phosphorus- and moisture-limited environments.** *Ann Bot* 2010, **105**:755-767.
 34. Suriyagoda LDB, Ryan MH, Renton M, Lambers H: **Above- and below-ground interactions of grass and pasture legume species when grown together under drought and low phosphorus availability.** *Plant Soil* 2011, **348**:281-297.
 35. Smith SE, Facelli E, Pope S, Andrew Smith F: **Plant performance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas.** *Plant Soil* 2010, **326**:3-20.
- This review discussed the implications of arbuscular mycorrhizal symbioses for plants dealing with abiotic stresses such as nutrient deficiency and water stress. The authors advocate to harness information and multidisciplinary approaches to understand the complex and multifaceted contributions of mycorrhizal symbioses.
36. Dodd IC, Ruiz-Lozano JM: **Microbial enhancement of crop resource use efficiency.** *Curr Opin Biotechnol* 2012, **23**:236-242.
 37. Benabdellah K, Abbas Y, Abourouh M, Aroca R, Azcón R: **Influence of two bacterial isolates from degraded and non-degraded soils and arbuscular mycorrhizae fungi isolated from semi-arid zone on the growth of *Trifolium repens* under drought conditions: Mechanisms related to bacterial effectiveness.** *Eur J Soil Biol* 2011, **47**:303-309.
 38. Porcel R, Barea JM, Ruiz-Lozano JM: **Antioxidant activities in mycorrhizal soybean plants under drought stress and their possible relationship to the process of nodule senescence.** *New Phytol* 2003, **157**:135-143.
 39. Tarafdar JC: **Response of arid legumes of VAM fungal inoculation.** *Symbiosis* 1997, **22**:265-274.
 40. Pellegrino E, Bedini S: **Enhancing ecosystem services in sustainable agriculture: Biofertilization and biofortification of chickpea (*Cicer arietinum* L.) by arbuscular mycorrhizal fungi.** *Soil Biol Biochem* 2014, **68**:429-439.
 41. Pang J, Wang Y, Lambers H, Tibbett M, Siddique KH, Ryan MH: **Commensalism in an agroecosystem: hydraulic redistribution by deep-rooted legumes improves survival of a droughted shallow-rooted legume companion.** *Physiol Plant* 2013, **149**:79-90.
 42. Sekiya N, Araki H, Yano K: **Applying hydraulic lift in an agroecosystem: forage plants with shoots removed supply water to neighboring vegetable crops.** *Plant Soil* 2011, **341**:39-50.
- This study designed a new agricultural system in the field to study hydraulic redistribution of perennial forage plants as 'donors' to the 'receiver' plants growing alongside them, with the shoots of 'donor' plants removed to minimise the effect of light-interception. This indicates water-use efficiency can be improved by the application of 'biological irrigation' and provides a potential pathway to improve crop production in water-limited environments.
43. Kimball BA, Kobayashi K, Bindi M, Sparks DL: **Responses of agricultural crops to free-air CO₂ enrichment.** *Adv Agron* 2002, **77**:293-368.
 44. Ainsworth EA, Rogers A, Blum H, Nosberger J, Long SP: **Variation in acclimation of photosynthesis in *Trifolium repens* after eight years of exposure to Free Air CO₂ Enrichment (FACE).** *J Exp Bot* 2003, **54**:2769-2774.
 45. Jin J, Tang C, Hogarth TW, Armstrong R, Sale P: **Nitrogen form but not elevated CO₂ alters plant phosphorus acquisition from sparingly soluble phosphorus sources.** *Plant Soil* 2014, **374**:109-119.
 46. Li P, Han X, Zong Y, Li H, Lin E, Han Y, Hao X: **Effects of free-air CO₂ enrichment (FACE) on the uptake and utilization of N, P and K in *Vigna radiata*.** *Agric Ecosyst Environ* 2015, **202**:120-125.
 47. Kant S, Seneweera S, Rodin J, Materne M, Burch D, Rothstein S, Spangenberg G: **Improving yield potential in crops under elevated CO₂: integrating the photosynthetic and nitrogen utilization efficiencies.** *Front Plant Sci* 2012:3.
 48. Evans JR: **Photosynthesis and nitrogen relationships in leaves of C3 plants.** *Oecologia* 1989, **78**:9-19.
 49. Dissanayaka D, Plaxton WC, Lambers H, Siebers M, Marambe B, Wasaki J: **Molecular mechanisms underpinning phosphorus-use efficiency in rice.** *Plant Cell Environ* 2018 <http://dx.doi.org/10.1111/pce.13191>.

This review focuses on membrane lipid remodelling coupled with hydrolysis of RNA and smaller P-esters in senescing organs, fuelling P remobilisation in rice, therefore improving P-use efficiency.

50. Jin J, Tang C, Armstrong R, Sale P: **Phosphorus supply enhances the response of legumes to elevated CO₂ (FACE) in a phosphorus-deficient vertisol.** *Plant Soil* 2012, **358**:91-104.

This study shows the interactive effects between elevated CO₂ and soil P supply on plant growth, emphasising the importance of soil P management in response to elevated CO₂ in order to harness the growth potential under CO₂.

51. Poorter H: **Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO₂?** *Global Change Biol* 1998, **4**:693-697.
52. Campbell CD, Sage RF: **Interactions between atmospheric CO₂ concentration and phosphorus nutrition on the formation of proteoid roots in white lupin (*Lupinus albus* L.).** *Plant Cell Environ* 2002, **25**:1051-1059.
53. Watt M, Evans JR: **Linking development and determinacy with organic acid efflux from proteoid roots of white lupin grown with low phosphorus and ambient or elevated atmospheric CO₂ concentration.** *Plant Physiol* 1999, **120**:705.
54. Haase S, Neumann G, Kania A, Kuzyakov Y, Römhild V, Kandeler E: **Elevation of atmospheric CO₂ and N-nutritional status modify nodulation, nodule-carbon supply, and root exudation of *Phaseolus vulgaris* L.** *Soil Biol Biochem* 2007, **39**:2208-2221.
55. Li B, Li YY, Wu HM, Zhang FF, Li CJ, Li XX, Lambers H, Li L: **Root exudates drive interspecific facilitation by enhancing nodulation and N₂ fixation.** *Proc Natl Acad Sci USA* 2016, **113**:6496-6501.

This study revealed a mechanism for intercropped maize promoting nitrogen fixation of faba bean, whereby maize root exudates increased nodulation and stimulated nitrogen fixation after enhanced gene expression. The results provide a novel mechanism for a positive relationship between species diversity and ecosystem productivity.

56. Gamper H, Peter M, Jansa J, Lüscher A, Hartwig UA, Leuchtmann A: **Arbuscular mycorrhizal fungi benefit from**

7 years of free air CO₂ enrichment in well-fertilized grass and legume monocultures. *Global Change Biol* 2004, **10**:189-199.

57. Treseder KK: **A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies.** *New Phytol* 2004, **164**:347-355.
58. Arndal MF, Merrild MP, Michelsen A, Schmidt IK, Mikkelsen TN, Beier C: **Net root growth and nutrient acquisition in response to predicted climate change in two contrasting heathland species.** *Plant Soil* 2013, **369**:615-629.
59. Cheng L, Booker FL, Tu C, Burkey KO, Zhou L, Shew HD, Ruffy TW, Hu S: **Arbuscular mycorrhizal fungi increase organic carbon decomposition under elevated CO₂.** *Science* 2012, **337**:1084-1087.
60. Suriyagoda LDB, Ryan MH, Renton M, Lambers H: **Adaptive shoot and root responses collectively enhance growth at optimum temperature and limited phosphorus supply of three herbaceous legume species.** *Ann Bot* 2012, **110**:959-968.
61. Hatfield JL, Boote KJ, Kimball BA, Ziska LH, Izaurralde RC, Ort D, Thomson AM, Wolfe D: **Climate impacts on agriculture: implications for crop production.** *Agron J* 2011, **103**:351-370.
62. Angus JF, Kirkegaard JA, Hunt JR, Ryan MH, Ohlander L, Peoples MB: **Break crops and rotations for wheat.** *Crop Pasture Sci* 2015, **66**:523-552.
63. Andresen LC, Michelsen A, Jonasson S, Schmidt IK, Mikkelsen TN, Ambus P, Beier C: **Plant nutrient mobilization in temperate heathland responds to elevated CO₂, temperature and drought.** *Plant Soil* 2010, **328**:381-396.
64. Long SP, Ainsworth EA, Leakey AD, Morgan PB: **Global food insecurity. Treatment of major food crops with elevated carbon dioxide or ozone under large-scale fully open-air conditions suggests recent models may have overestimated future yields.** *Philos Trans R Soc Lond B Biol Sci* 2005, **360**: 2011-2020.
65. Thorup-Kristensen K, Kirkegaard J: **Root system-based limits to agricultural productivity and efficiency: the farming systems context.** *Ann Bot* 2016, **118**:573-592.